

TEMPORAL PATTERNS OF SEXUAL AND ASEQUAL  
REPRODUCTION IN THE COLONIAL ASCIDIAN  
*METANDROCARPA TAYLORI* HUNTSMAN<sup>1</sup>

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*Metandrocarpa taylori* is a colonial ascidian common on rocks in the low intertidal zone along California shores. Reddish-orange colonies spread out in flat sheets, often covering large expanses of granite rocks, particularly on their lower surfaces. Individuals, which resemble small simple ascidians, are joined to one another basally by a thin layer of test containing blood vessels.

Previous studies on *M. taylori* have been concerned largely with bud development (Abbott, 1953), analysis of the factors involved in bud initiation (Newberry, 1965), and larval structure and behaviour (Abbott, 1955).

The major objective of the present work is the comparison of sexual and asexual reproductive activities in *M. taylori*, including consideration of how these two processes interact in colonies throughout the year. There is also a brief consideration of the seasonal aspects of reproduction in relation to water temperature and phytoplankton. A study of the gonads was also necessary in order to determine criteria for sexual reproductive activity. Except for the observation of Abbott (1955) that larvae settled in the summer months, nothing has been recorded as to the extent of either the sexual or asexual reproductive cycle. Likewise, there is no adequate description of the gonads in the literature; Huntsman (1912) and Ritter and Forsyth (1917) described populations of *M. taylori* that differed somewhat from each other in the number and arrangement of the gonads.

MATERIALS AND METHODS

Specimens of *Metandrocarpa taylori* used in the study of sexual reproduction were collected at Pescadero Point, Monterey County, California (36°31'47"N.) at approximately two week intervals from June 1, 1961 to June 2, 1962. Colonies were sampled by using a chisel to remove clusters containing about a dozen individuals each. Approximately ten different colonies were sampled on each collecting date. The specimens were relaxed for 12-24 hours in a 7% MgSO<sub>4</sub>-seawater solution, then fixed in Bouin's fluid and stored in 70% EtOH. Adults in each cluster, connected basally by a common tunic, are readily separated from one another intact. Gonads are easily exposed by removing the upper half of the zooid by a horizontal cut, then carefully lifting out the remaining portion of the branchial basket along with the stomach and intestine.

Since *M. taylori* usually occurs on irregular surfaces in situations where growth is difficult to monitor, colonies used in the study of asexual reproduction were established on glazed tiles and maintained in racks attached in the intertidal zone adja-

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cent to Hopkins Marine Station. Three clusters of adult zooids from separate colonies were collected each month at Pescadero Point, cleaned of debris, and tied with thread to the center of six-inch square glazed ceramic tiles. Tiles were kept in running seawater for a month in the lab, to allow the zooids to attach and begin to bud. The tiles were then placed in slotted redwood boxes bolted to intertidal rocks protected from heavy surf approximately 0.2 feet above mean lower low water.

Once a month, all of the tiles bearing cultures were transferred to laboratory aquaria, observed, photographed with a Polaroid camera, and returned to the sea boxes within 24 hours. Individual colonies were maintained until they grew to the edges of a tile. While there was some damage and loss of colonies due to storms, most colonies expanded to cover one side of the tile by the end of four months in the intertidal zone.

The gonads of twenty adult zooids collected biweekly from different colonies were measured to provide data on sexual reproduction. Female gonads were assigned to the following size classes: small (ovaries less than 0.1 mm in diameter); medium (ovaries 0.1 mm or more in diameter, eggs still encased in ovarian epithelium); and developing (mature eggs and various stages of embryos, both lying free in the mantle cavity). Size classes for testes were small (less than 0.2 mm in greatest diameter); medium (0.2–0.4 mm), and large (over 0.4 mm).

## RESULTS

### *Gonads*

In *Metandrocarpa taylori* the separate testes and ovaries are partially embedded in the ventral floor of the mantle cavity. The ovaries extend in a horseshoe shape, back and outward on both sides of the medial endostylar ridge. The testes extend posteriorly from these on each side, in a line on the right but bunched on the left due to presence of the stomach. The gonads are illustrated in Haven (1965). The average number of ovaries was seven (range 0–13) and the average number of testes was nine (range 0–17). The number and the arrangement of gonads in *Metandrocarpa taylori* are in general accord with the reproductive system described by Ritter and Forsyth (1917) for *M. michaelseni*, a species placed in synonymy with *M. taylori* by Abbott (1953).

In animals not actively engaged in sexual reproduction the ovaries are small (less than 0.1 mm in diameter) and contain developing eggs in early stages. Three or four enlarging eggs lie in each ovary. As the eggs enlarge and become yolky, they stretch the overlying epithelium. No more than one or two eggs are fully mature at the same time in an individual ovary and it appears that usually only one egg is released at a time from an ovary.

When the eggs reach a diameter of approximately 0.3 mm they are released from the ovary, apparently by rupture of the gonad epithelium since an oviduct is lacking, and come to lie free in the mantle cavity. Fertilization probably occurs at this time. The larvae are usually retained in the adult until they are capable of swimming away to settle (Abbott, 1955).

Small testes (less than 0.2 mm in diameter) have a rounded base and a vas deferens protrudes from the center of each. Sections of testes of this size show

densely packed cells with no lumen evident. Testes of intermediate sizes (0.2 mm–0.4 mm in diameter) are pear-shaped. Smears of these testes show many nurse cells with attached spermatids, together with immature sperm. With further enlargement (over 0.4 mm diameter) the testes develop lobulations, and smears contain a good proportion of highly motile sperm. Collections frequently contained a number of adult zooids with no visible testes, suggesting the possibility of complete regression of the testes during periods of inactivity.

*Sexual reproduction in the population*

The annual pattern of sexual reproductive activity, based on the most advanced stages of gonads present in individuals, is shown in Figure 1. Sexual reproduc-

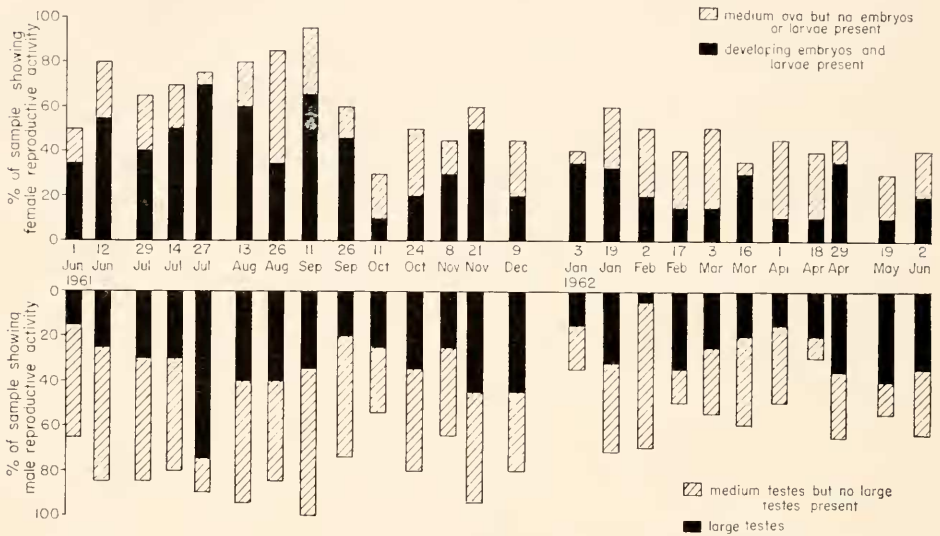


FIGURE 1. Sexual reproductive activity of *Metandrocarpa taylori* in the collections of 1961–1962. Zooids are classed according to the most advanced condition of reproductive activity of the male and female systems present. Dates of collection are shown on the horizontal scale.

tion continues throughout the year. At least 10% of the population always showed some developing embryos and larvae, and these stages were present in a maximum of 70% of the sample in the collection of July 27, 1961. In addition, medium sized eggs were present in other individuals from 5% to 50% of the time. At no time was less than 30% of the population engaged in sexual reproduction, as indicated by the presence of medium sized eggs and/or developing embryos and larvae. Summer was the period of greatest sexual activity. In the three month period from June 12, 1961 to September 11, 1961, an average of 79% of the population contained medium sized eggs or developing larvae or both and the number of individuals containing developing embryos and larvae was 30% higher than in the remainder of the year.

The lower half of Figure 1 shows the condition of the testes in each collection. During the summer, when embryo production was increased, there was no corresponding increase in the proportion of individuals with large testes, but increased summer activity is indicated when the classes with medium sized and large sized testes are considered together. Throughout the year a rise or fall in the incidence of medium and large testes usually corresponded to a similar change in the incidence of medium sized and developing eggs; the correlation coefficient for this was highly significant ( $r = 0.784$ ;  $P < 0.0005$ ).

Collections of *M. taylori* taken by Dr. Donald P. Abbott of Stanford University from April 1949 to March 1950 were similarly analysed and also showed greater sexual reproduction during the summer months and early fall.

TABLE 1

*Summary of egg and testes stages present simultaneously in individual zooids*

Individual Zooids with:	Collections of 1949-50 period (N = 440)	Collections of 1961-62 period (N = 540)
No ovary visible	13%	1%
Small eggs only	43	45
Small + medium sized eggs	11	20
Small, medium sized and developing eggs	9	13
Medium sized + developing eggs	15	16
Developing eggs only	4	2
Small + developing eggs	3	2
Medium sized eggs only	2	1
Total	100%	100%
No testes visible	10%	10%
Small testes only	22	21
Small + medium testes	10	3
Medium testes only	30	35
Medium + large testes	11	8
Large testes only	17	23
Total	100%	100%

Goodbody (1961) has questioned the measurement of gonad conditions in ascidians as an accurate measure of sexual activity, citing resorption of unfertilized winter eggs in *Botryllus schlosseri*. However, larvae of *M. taylori* settled throughout the year on glass slides kept in the intertidal zone at Hopkins Marine Station by Dr. A. T. Newberry, University of California, Santa Cruz (personal communication). Therefore, dormancy or arrested development is unlikely in the present case. Also, the peak occurrences during the year of individuals just completing a phase of sexual reproduction (*i.e.* having medium and developing but no small eggs) corresponds to peaks of individuals entering such a phase (having small and medium eggs only) three weeks previously. This suggests that eggs are not held in a dormant state, but become developing embryos and larvae in a predictable period of time. The fluctuations in the occurrence of zooids entering a period of

sexual reproduction (those having small and medium eggs) lend support to the reality of the seasonal variations in sexual reproduction shown in Figure 1.

A remarkably large reservoir of small eggs is present in the population throughout the year. This reserve is quite constant and is only slightly depleted during periods of increased sexual reproduction. This is partly because a zooid appears to replace almost immediately any small eggs that develop during a period of active sexual reproduction.

The portion of the population containing at least some small testes is relatively low most of the year. Individuals with medium sized testes form the most frequent male component in the population. It is possible that less time is required for a small egg to enlarge and be released from an ovary than for a small testis to enlarge and produce ripe sperm. If this is the case, the more immediately available reserve of male gonads would necessarily be the individuals with medium sized testes.

#### *The reproductive condition in individual zooids*

Because the adult zooid is opaque, the sequence of reproductive events cannot be determined directly by repeated observations on particular individuals. However, since individual zooids may contain simultaneously eggs, testes, and embryos in several different stages of growth, inferences can be made about the sequence of gonad development, including the relationship of male to female gonad development within individuals.

Analysis was made of egg stages present simultaneously in 980 individual zooids (Table I). When a zooid is reproductively active, the eggs within are usually in more than one class and these classes represent developmental stages that are in sequence with one another. The data suggest the following sequence of egg development within the zooid. When a zooid is not reproductively active, each ovary contains several small eggs. With the onset of reproduction, these eggs enlarge; individuals containing both small and medium sized eggs represent this point in the life history of a zooid. Later, all three stages of eggs can be found, and finally all the small eggs enlarge and individuals contain only medium sized and developing eggs. However, before this batch of eggs is entirely released, small eggs again appear in the ovaries. The data cannot show whether individual zooids ripen eggs more than once during a period of active reproduction of the colony as a whole.

The size classes of testes present simultaneously in individuals are summarized in Table I. In 85% of all the individuals examined, the testes fall into one size class. In the remainder of specimens, where more than one size class of testes was present, the size classes were developmentally adjacent. This indicates that all the testes within an individual usually enlarge simultaneously, or at least in relatively close synchrony with one another.

Within individual zooids the development of testes and ovaries is positively correlated. Most of the time, when eggs are small or ovaries are not visible, the testes are small or not visible grossly. When eggs have begun to enlarge in the individual, the testes are usually medium and/or large. The per cent of individuals with large testes increased with the presence of developing eggs, and reaches a peak in zooids containing only medium sized and developing eggs.

Whether or not self-fertilization occurs in *M. taylori* is unknown, but since the colonies appear to be clones that are established asexually from a single meta-



morphosed larva, cross-fertilization within the colony would be equivalent to self-fertilization.

### *Temporal patterns of asexual reproduction*

*Metandrocarpa taylori* is a colonial tunicate, of the "social" type, with zooids connected basally, but each individual having a separate covering of test. Colonies are produced asexually by pallial budding along the free basal margins of the mantle (for details of bud growth and differentiation, see Abbott, 1953). Throughout its life the newly budded zooid maintains contact with its parent and with its own subsequent bud progeny by means of blood vessels traversing the tunic-covered connections between them. Buds are projected far enough from the parents so that there is room for eventual enlargement to adult size. In a colony growing on a clean, unobstructed surface an additional distance of approximately two millimeters separates young zooids. This allows large areas to be fairly rapidly colonized, the spaces within the colony being filled later by intercalary budding.

Zooids used to establish experimental colonies were taken from mature colonies in the field and were closely packed, with basal margins fused throughout. These zooids were not actively budding at the time of collection, since new buds arise only from areas on zooids where the basal test margin is free, and not fused to that of adjacent zooids (Abbott, 1953). When the test margins were freed at the edges of the clumps of adults used to establish new colonies on tiles, most of the clusters began to produce buds. The ability to produce buds appears to be potentially present in zooids of *M. taylori* throughout life.

New colonies were established on tiles each month for a year, to provide a continuous and overlapping record of asexual reproductive activity. Figure 2 shows the form and history of a typical colony cultured in the intertidal zone for four months. The adults which founded the colony are centrally located. New growth radiated outward from these original zooids as buds appeared on the periphery. As the colony grew larger, the older zooids toward the center of the colony also enlarged, and their test margins coalesced, with some intercalary budding filling most of the remaining space. Thus the center of the colony became more and more solidly packed with zooids and produced no more buds after reaching this packed condition.

Photographs taken each month of each colony cultured on a tile provided a series of growth records extending throughout a year. As the first step in translation of these records into statistical data, areas of new growth each month were outlined and mapped in diagrammatic tracings made from the original photographs. The vascular connections retained between each zooid and its parent allowed the determination of the lineage of all new buds grown during a month. A bud was counted as a new zooid only when its budstalk attachment to its parent was clearly broken. Once the growth was outlined, the zooids were classified as to their order of descent. In Figure 2, zooids enclosed within a heavy line are part of the base population present at the end of the previous month. Zooids giving rise directly to new growth, lying outside of a heavy line, are termed "budding adults." Buds ("descendants") produced during the month are assigned generation numbers in relation to the budding adult of the previous month from which they stem; those

buds arising from a budding adult are considered "first generation," and all of the buds traceable to them during a month are on a single "clonal line."

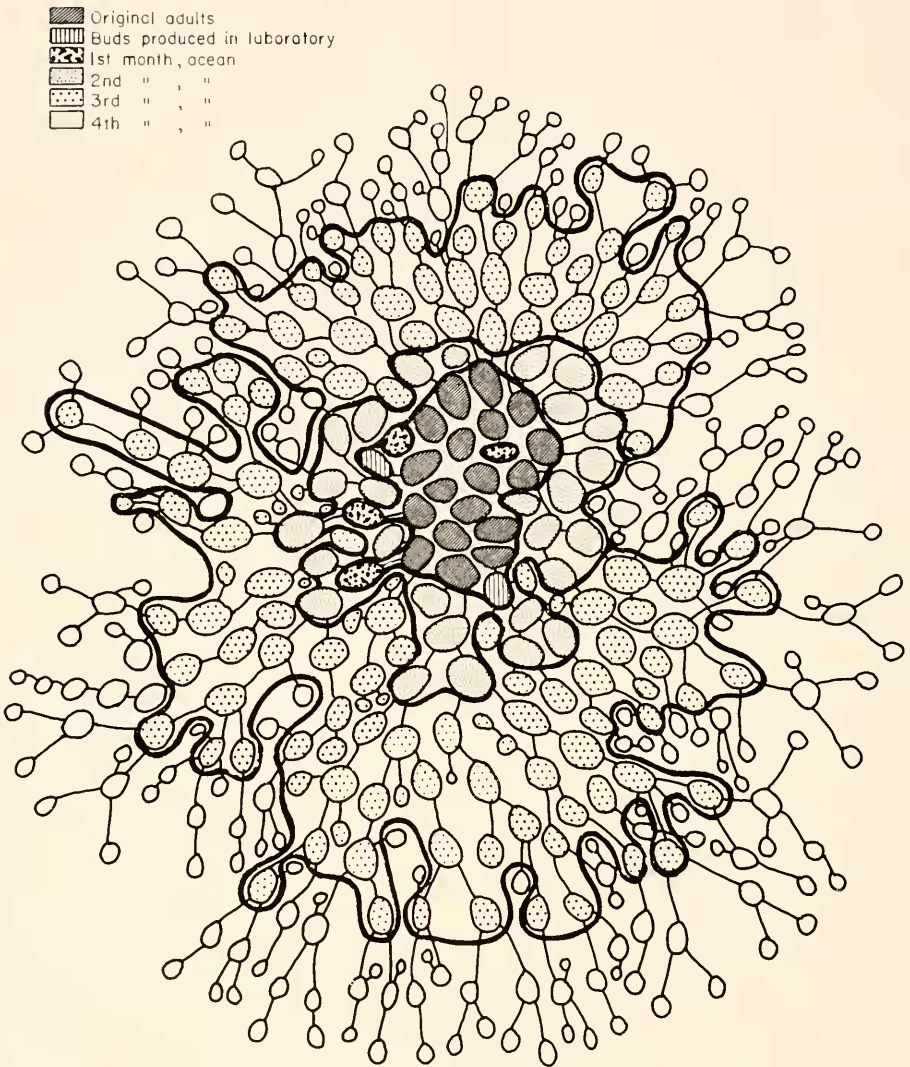


FIGURE 2. Budding pattern of a colony of *Metandrocarpa taylori* cultured on a glazed ceramic tile for four months in the intertidal zone. Growth during each successive month is circumscribed by a darkened contour line.

In measuring growth rate, only budding rate expressed as average number of descendants produced per budding adult during the month expressed growth in a meaningful way. This was calculated by dividing the total number of new individuals produced during the month by the number of budding adults giving rise to

them; the final calculation expressed as number of descendents per budding adult per day.

### *Effects of colony size and age*

Two aspects of a colony, its size and its age, might be expected to affect budding rates. With respect to size, the adults in the interior of a colony usually have no room to bud but they might provide an additional source of nutrition to budding zooids at the colony margin through the anastomosing vascular network of the colony. If this were the case, a large colony, with a high percentage of non-budding adults, might be expected to bud at a faster rate than smaller colonies. Data from all months were pooled to see if any correlation existed between budding rate and colony size. There was none. Of course, the *number* of adults that do bud and produce a month's growth is clearly related to the size of a colony. This positive correlation is due to the expansion of the periphery of the colony (where most budding adults occur) as the total size (area) of the colony increases.

With regard to the effect of age on budding rate, determinations of average growth rate for any particular month of the year were based on growth occurring in colonies on tiles that had been in the ocean for differing amounts of time. Neither the zooids nor colonies as whole units appear to have a fixed life span, as do some tunicates; while adult zooids do die from time to time, a colony of *Metandrocarpa taylori* does not undergo periodic fluctuations in population due to death of adult zooids. The possibility remains, however, that there may be other effects of growth rate due to the age of a colony.

Data on the budding activity for colonies that had grown for similar lengths of time in the ocean (regardless of season), showed that the budding rate of colonies during their first month in the intertidal zone (0.77 buds/budding adult/day) was significantly lower than that found in any of the succeeding months. This lowered rate of growth probably represents a period of acclimation, since the colonies had previously been in laboratory tanks for a month. Since this rate does not reflect any conditions of growth that might be encountered in field populations of *M. taylori*, seasonal budding rates in all instances have been based on growth occurring in colonies *after* this first month in the intertidal zone.

Budding rates in colonies during their second, third, and fourth months in the ocean were 0.122, 0.125, and 0.135 buds/budding adult/day, respectively. An analysis of variance showed that the differences between these rates were not significant ( $F_{2,45} = 0.245$ ). Only one colony provided data on growth during the fifth month in the ocean (0.111 buds/budding adult/day).

### *Annual pattern of asexual reproduction*

Asexual reproduction is exhibited throughout the entire year in colonies of *Metandrocarpa taylori* cultured in the intertidal zone (Fig. 3A). There is, however, marked variation in average monthly budding rates during this period. Budding activity was high in June 1961, but declined rapidly thereafter and continued at a slow rate for the rest of the summer, coming virtually to a standstill in September. A burst of asexual reproductive activity followed in October and budding rates remained high during the remainder of the year under study with



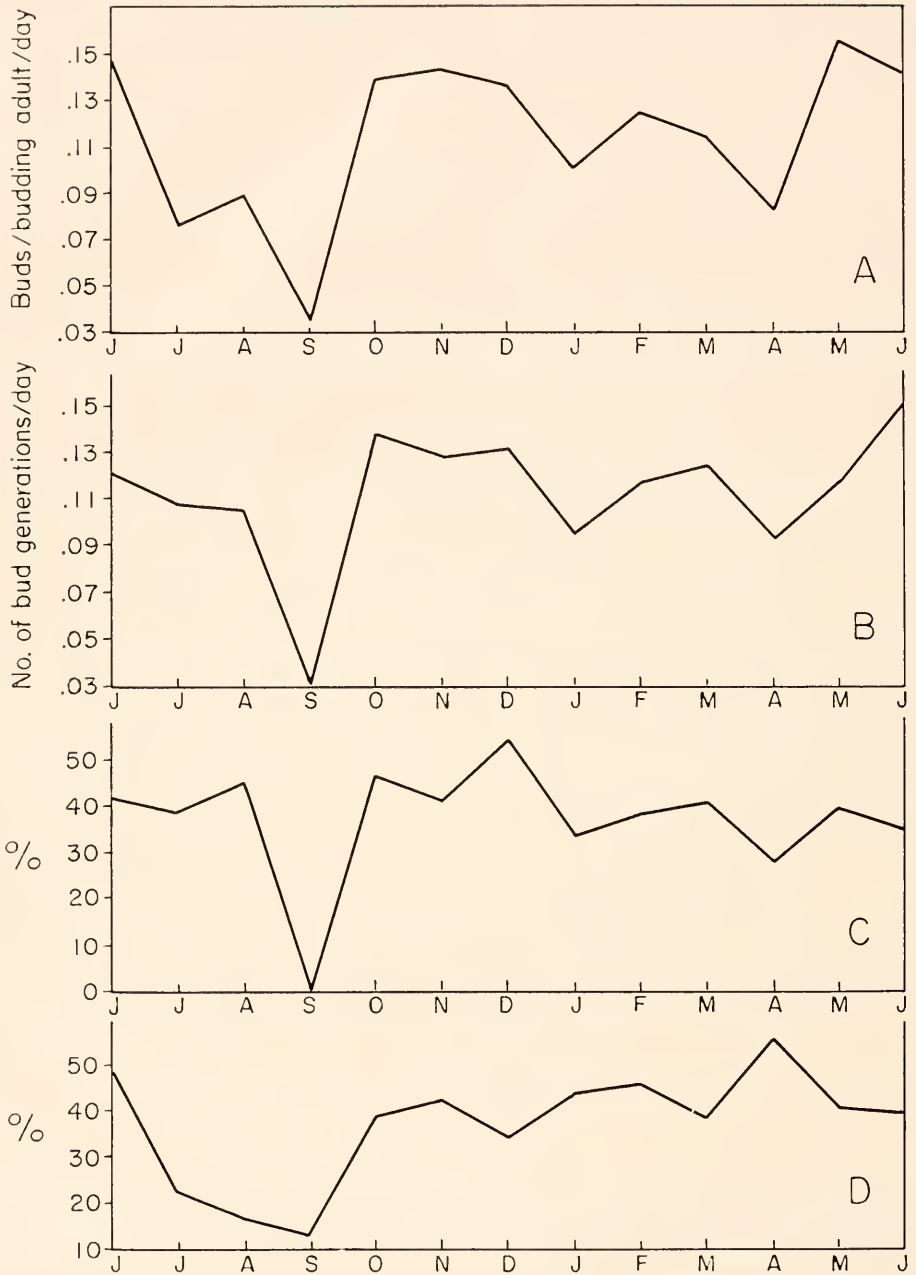


FIGURE 3. Comparative activity of components determining budding rate; (A.) average monthly budding rate in colonies of *M. taylori*; (B.) average of maximum number of bud generations produced per day; (C.) average per cent of zooids produced during a month that in turn produced buds; (D.) incidence of multiple budding: average per cent of all zooids producing buds during a month that gave rise directly to more than one bud.

the exception of a drop in budding rates during April, 1962. Budding activity at this time was lowered to a rate comparable to that evidenced in the previous August. An apparent drop-off in budding rates occurred during January. In this case, however, growth rate is based on measurements in a single colony, and the drop is of dubious significance.

#### *Components of growth rate change within a colony*

An analysis of budding activity in *Metandrocarpa taylori* shows that there are three ways in which a colony may vary its rate of bud production in a given period of time: (1) the rate at which successive bud generations follow one another may vary, so there is a change in the number of bud *generations* produced per unit of time. (2) The average number of bud offspring produced directly by those zooids which bud may vary with the season; *i.e.*, during certain periods the incidence of twin and triplet bud offspring may be greater than at other times. (3) The number of terminal budding adults which fail to bud at all may vary with the season. An increase or decrease in any one of these would affect the total rate of bud production. If all of these methods were more or less equally involved in producing changes in budding rate, asexual reproduction might then be considered directly related to the overall metabolism of a colony (interactions with sexual activity being ignored for the present analysis). If, however, the relative roles of each of these factors involved in budding rates shifts from time to time, a more complex picture of the components involved in colony growth emerges. An analysis of each of the factors follows.

(1.) *Maximum number of generations produced per unit time.* The maximum rate of production of new zooid generations each month (Fig. 3B) varies in parallel with overall colony growth rate throughout the year (Fig. 3A). Bud generation time varies inversely with colony growth rate. For example, the bud production rate for September of one generation in thirty days contrasts with a rate of one generation every six days in October.

(2.) *Incidence of multiple budding.* All zooids that are not terminal on a clonal line have given rise to at least one bud. The spreading pattern of growth encountered in colonies is accomplished by the production of two or more buds on the part of at least some of the parental zooids. Occasionally, as many as six buds have been found coming from a single zooid. The zooids that produced buds during a given month (including the budding adults that were parental to the first generation of buds) were divided into two categories: those zooids that produced only one bud, and those that produced two or more buds. The seasonal trends in overall budding activity and the incidence of multiple budding (Fig. 3D) are similar (low in the summer and high in the winter). However, fluctuations within the seasons show little relation between the two rates.

(3.) *Per cent of buds becoming parental.* During the year under study, an average of 40% of zooids that were produced each month in turn produced buds during that month. However, the variation found ranged from an absolute minimum in September, to a high point in December, when 55% of the zooids produced during that month gave off buds. When this rate is compared with the annual budding rate (Fig. 3C) there are similarities in the direction of change (*i.e.*, in-

crease or decrease), but the amount of this change for corresponding periods in the two curves sometimes differs widely (*e.g.*, June–July, 1961; April–May, 1962).

The effect of changes of activity in the three components of budding on overall budding rate is more clearly observed in those months in which budding rate rose or fell markedly in relation to the previous month. Major changes in budding rate in colonies of *Mctandrocarpa taylori* frequently involve parallel shifts in all of the three growth components enumerated. However, during three of the months, budding rate changes are accounted for by shifts in the number of generations produced and the number of new buds that became parental, but not in the amount of multiple budding taking place.

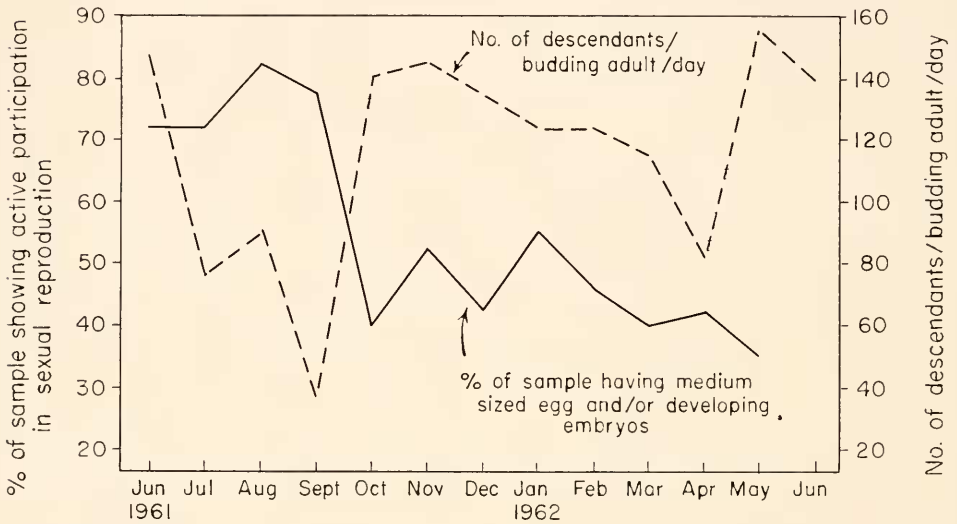


FIGURE 4. Monthly average budding rate in cultured colonies of *M. taylori* during 1961–62 compared with sexual reproductive activity in field populations during the same period.

#### *Comparison of sexual and asexual reproductive activity*

Both sexual and asexual reproduction occur throughout the year in *M. taylori*. The seasonal interrelationships of the two modes of propagation are outlined in Figure 4. In late summer and early fall, sexual reproduction is at its highest level, while asexual reproduction is declining toward its minimum. For the remainder of the year, while sexual reproduction is fluctuating at a relatively low level, asexual reproduction is, for the most part, at a relatively high level. The most striking changeover occurs during the sudden step decline of sexual reproduction in late September–early October. During the same period, there is an equally large and sharp increase in asexual reproduction.

#### *Correlation of reproductive patterns with temperature and food*

Giese (1959) notes that reproductive cycles may be the result of endogenous factors, exogenous factors, or a combination of both. Nothing is known of endog-

enous factors in *Metandrocarpa taylori* that might account for cyclic reproduction. The exogenous factors often considered to influence sexual reproduction in marine organisms are cited by Giese: light, salinity, temperature and food. Salinity changes very little during the year in Monterey Bay, the average annual range (based on a seven-year period) representing a variation of less than one part per thousand (Bolin and Abbott, 1963). The other two factors are considered here. Phytoplankton records are based on plankton hauls averaged for six stations in Monterey Bay taken each week by the Hopkins Marine Station vessel TAGE, working under the auspices of California Cooperative Oceanic Fisheries Investigations program.

In 1961-62 there is a general direct relationship between sexual reproductive activity in *M. taylori* and ocean temperatures (Fig. 5). In summer and early fall, when temperatures were high, sexual reproduction was also high, reaching a peak in September when 96% of the sample showed reproductive activity. During the

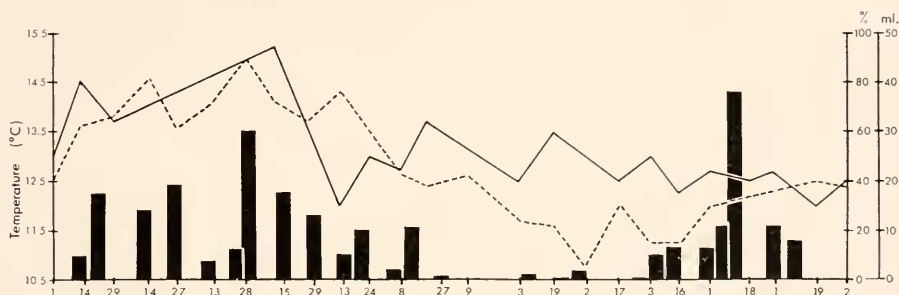


FIGURE 5. Seasonal changes in temperature and phytoplankton crop in relation to sexual reproduction in *M. taylori*. Solid line indicates per cent of sample containing medium sized eggs and/or developing embryos and larvae. Dashed line shows daily shore temperatures taken at Hopkins Marine Station averaged for period preceding each collection. Bars indicate average phytoplankton volumes (milliliter wet settled phytoplankton/haul) in Monterey Bay.

winter and spring, when water temperatures were low, sexual activity fluctuated about a relatively low mean value of about 45%. The correlation coefficient ( $r$ ) for temperature and sexual reproductive activity (per cent of sample containing medium and/or developing eggs) was positive and highly significant:  $r = 0.616$ ,  $P < 0.005$ . The correspondence between temperature and sexual reproductive trends, however, is not exact enough to allow the conclusion that temperature is the only important controlling factor. Only half of the time were rising water temperatures accompanied by increased sexual reproduction during 1961-62, and a drop in average ocean temperature was mirrored by a decrease in sexual activity in only one-third of the cases. In particular, there was no abrupt change in temperature with which the very sharp drop in sexual activity occurring in late September could be correlated.

When budding activity in the cultured colonies was compared with the average shore temperatures for the same period, there was a general inverse relationship between the two. However, temperatures and asexual reproduction showed little detailed correspondence throughout the year, and this suggests that the effects of



temperature, if any, are indirect and asexual reproductive activity is influenced by other factors.

Phytoplankton crops along the central California coast are highest during the summer months, a time when sexual reproduction is particularly marked in populations of *M. taylori* (Fig. 5). Summer phytoplankton volumes reached a peak in early September in 1961 and sexual reproductive activity was highest soon thereafter. However, the relationship between phytoplankton crop and amount of sexual reproduction does not appear as direct when conditions during the winter and spring months are taken into consideration. For example, sexual activity rose late in January without any apparent change in minimal phytoplankton levels. Conversely, a marked bloom of phytoplankton in mid-April was not accompanied or immediately followed by a rise in sexual reproductive activity.

When budding activity was compared with phytoplankton volumes there was no direct relationship found.

#### DISCUSSION

The finding that the colonies of *Metandrocarpa taylori* reproduce sexually throughout the entire year is not totally unexpected considering that the eggs are yolky, and the larvae are brooded until fully developed. Furthermore, the larvae are wholly lecithotrophic, and more than 50% of them settle within two hours after release from the parent (Abbott, 1955). In invertebrates breeding in such a manner, with the larvae undergoing nonpelagic development, species are likely to exhibit a prolonged breeding season (Giese, 1959) and may spawn during the whole year (Thorson, 1946).

Although phytoplankton has seasonal blooms, there is an abundant food supply available to *M. taylori* during the entire year. Glynn (1965) made periodic samples of water washing over the intertidal zone during high tide in the Monterey Bay area. The results showed that there is a good supply of organic detritus suspended in shore waters throughout the year. This material is particularly abundant during the winter and spring months, a time when phytoplankton crops are minimal; in this period organic materials, such as kelp and other seaweeds, are torn loose and churned up by storm waters (Booolootian, Giese, Farmanfarmaian and Tucker, 1959). MacGinitie (1937) points out that an abundance of food may be available to ciliary-mucoid feeders, since even bacteria can be successfully captured. *Metandrocarpa taylori*, a ciliary-mucoid feeder, has available to it phytoplankton, bacteria and organic detritus that is suspended in inshore waters.

Sometimes simultaneous sexual and asexual reproduction may occur in animals with a life span shorter than a year (Berrill, 1951). This serves to heighten the interest in what occurs in *M. taylori*, in which the colony has no known definite life span and survives longer than annual forms. Asexual reproduction in *M. taylori* represents a type of growth, and this species falls in the general category of organisms, recognized by Orton (1920), in which major periods of growth occur in the non-breeding season.

The lower intertidal zone where *Metandrocarpa taylori* is found in the field is replete with invertebrates, and the rocks are seldom bare except when tossed about and scoured during winter storms. Winter turbulence could make it more difficult for larvae of *M. taylori* to settle. Also, the impact and the scouring action of waves

might reduce the chances of survival of juvenile animals on the rocks during the winter. If this is true, there may be a mild selective pressure toward reduction of sexual reproduction during the winter. Budding would certainly be advantageous during this time as a means of recouping losses to colonies due to scouring action and increasing areas colonized. This may in part explain the selective value of continuous reproduction in *Metandrocarpa taylori*, with alternate stress on sexual and asexual methods.

In other styelid ascidians studied, seasonal breeding has been commonly noted; *Pelonaia corrugata*, deep off the Scottish coast breeds for only two to four weeks in January or February (Millar, 1954a) and *Styela rustica*, off the coast of Sweden has a similarly abbreviated breeding period during January and February (Lützen, 1960). On the other hand, longer periods of reproduction, extending roughly from spring to fall, are found in *Styela coriacea* off the northern German coast (Diehl, 1957), and *Dendrodoa grossularia* in shallow Scottish coastal waters (Millar, 1954b). *Styela plicata* has both a spring and a fall breeding season, where it occurs in the Lagoon of Venice (Sabbadin, 1957). In contrast to the breeding seasons noted above, *Symplegma viride*, a tropical-subtropical species and the only styelid tunicate among those listed here which reproduces both sexually and asexually, breeds throughout the year on the coast of Jamaica (Goodbody, 1961).

Reproductive cycles in two other ascidians of the Monterey area have been recorded. Trason (1963) found reproduction in *Pycnoclavella stanleyi* similar to that noted in the present study; both sexual and asexual reproduction occur throughout the year, with sexual reproduction occurring more actively in summer months. Levine (1962) reports cyclic sexual reproduction in *Eudistoma ritteri*, with larvae produced from mid-April to September.

Three invertebrates, other than ascidians, have been found that breed continuously and with little apparent fluctuation in the Monterey area; these are the red abalone, *Haliotis rufescens* (cf. Boolootian, Farmanfarmanian, and Giese, 1962), the kelp crab, *Pugettia producta*, and the porcelain crab, *Petrolisthes cinctipes* (cf. Boolootian *et al.*, 1959). These findings correspond to Giese's observation (1959) that, although a restricted period of breeding seems to be the general case in marine invertebrates, most invertebrates in temperate seas spawn over a much longer period of time than do those living in polar regions, and in a few temperate region species, spawning may last for the greater part of the year.

Most marine animals investigated thus far in the Monterey area have well-defined breeding seasons, and the majority spawn in the spring and summer months. In these cases, the free-swimming larval stages, unlike those of *Metandrocarpa taylori*, are plankton feeders which get into open waters where organic detritus is scarcer than near the shore, necessitating a reproductive cycle that is geared to the phytoplankton bloom.

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## SUMMARY

1. *Metandrocarpa taylora* Huntsman (1912) is an ovoviviparous colonial ascidian with separate zooids connected by a common basal tunic, which reproduces asexually by pallial budding.

2. Specimens in collections from field populations show maximum periods of sexual reproduction during the summer months. Although approximately 80% of the 1961 summer samples were reproductively active during this period, sexual reproduction continued during the remainder of the year with no less than 30% of the population active at any time. Eggs and testes develop simultaneously within the individual zooids.

3. Asexual reproduction was quantitatively studied in colonies cultured in the intertidal zone. Budding rates are lowest during the summer and continue at a high level during the remainder of the year. These rates are not dependent upon the size or age of the colony, but do derive from variations in rates at which successive bud generations follow one another and from the number of bud offspring produced by each zooid.

4. Although the two modes of reproduction are not mutually exclusive, it is clear that one form predominates in activity during any single season.

5. There is a general direct relationship between sexual reproductive activity and ocean temperature. There is little correlation of reproductive activity with food supply, since either phytoplankton or suspended organic detritus are abundant in Monterey Bay all year.

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